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Review

FOOD WEB STRUCTURE AND BIOGENIC CARBON EXPORT ON THE CONTINENTAL SHELVES OF THE ARCTIC OCEAN*

Louis LEGENDRE[1], Richard B. RIVKIN[2] and Christine MICHEL[1]

[1] *Département de biologie, Université Laval, Québec, Québec G1K 7P4, Canada*
[2] *Ocean Sciences Centre, Memorial University of Newfoundland, St. John's, Newfoundland A1C 5S7, Canada*

Abstract: The Arctic Ocean is circumscribed by the North American and Eurasian continents. These land masses have an extensive system of continental shelves which receive the outflow of several major rivers and are covered by sea ice for most of the year. In this paper, we propose that a unique combination and chronology of environmental conditions are responsible for the structuring of food webs and the concomitant patterns of biogenic carbon export on the Arctic Ocean continental shelves. First, we examine the general environmental characteristics of polar waters (extreme seasonal cycle of solar radiation and submarine irradiance, low temperature, seasonal ice cover), the specific conditions that exist on Arctic Ocean continental shelves (riverine inputs, shelf-basin exchanges), and the general structure of pelagic marine ecosystem as well as that typical of Arctic shelves. Second, we discuss the significance of the unique food web structure on Arctic shelves with regard to biogenic carbon export to apex predators and sequestration at depth. We present evidence that the extensive shelf system and riverine inputs influence the structure and dynamics of Arctic marine food webs in four ways. First, the large freshwater runoff delivers particulate material and dissolved inorganic and organic nutrients, it lowers the salinity and favors the development of sea ice. Second, because of the extreme annual cycle of solar radiation, there is a brief pulse of primary production, which is often followed by periods of rapid sedimentation of particulate organic carbon. Third, because of low seawater temperature, there is slow oxidation of particulate organic matter in the water column and on the bottom. The latter provides a supply of organic and inorganic nutrients for the maintenance of a microbial trophic level in the water column. Low temperature may favor efficient transfer of microbial components towards larger pelagic grazers and, ultimately, to apex predators. Fourth, the seasonal ice cover constrains biological activity, provides a refuge and habitat for microorganisms and small animals, and reduces ocean-atmosphere interactions thus favoring the sequestration of biogenic carbon.

1. Introduction

The North and South polar seas share a number of common environmental characteristics. For example, in both environments, the pattern of solar radiation is highly seasonal, seawater temperatures are persistently low, and the oceans are ice-covered for a large part of the year. However, unlike the Southern Ocean, the Arctic Ocean is circum-

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scribed by land masses and there is an extensive system of continental shelves which receive the outflow of several major river systems from the North American and Eurasian continents. The surface area of the Arctic ocean (including Hudson Bay) represents only 5% of the World Ocean, but it accounts for *ca.* 25% of all continental shelves. These geomorphological and fluvial characteristics have profound effects on water circulation patterns, seawater nutrient chemistry, the chronology of sea ice formation, the cycling of carbon through the biota, and ultimately the rates and patterns of biogenic carbon sequestration. This paper first examines the general environmental characteristics of polar waters, the specific conditions that exist on Arctic Ocean continental shelves, and the general structure of pelagic marine ecosystems as well as that typical of Arctic shelves. Second, it discusses the significance of the unique food web structure on Arctic shelves with regard to biogenic carbon export to apex predators and sequestration at depth.

2. Environmental Characteristics of Polar Waters

2.1. Irradiance

Light, nutrients, and temperature all influence the development of algal populations in polar regions, however light intensity appears to be the most important environmental factor for algal growth. The unique annual cycle of solar radiation constrains cycles of primary production in both the Arctic and Antarctic (PALMISANO *et al.*, 1987; SMITH *et al.*, 1988; WELCH and BERGMAN, 1989; RIVKIN, 1991). At high latitudes, for example in for McMurdo Sound, Antarctica (78°S), and Resolute Passage, Canadian High Arctic (75°N), four months of continuous darkness are separated from an equal period of continuous light by a transition during which the photoperiod rapidly changes (by up to 20 min per day). During summer, maximum irradiance at high latitude is only 60–75% of that at mid latitudes (*e.g.* 2000 μmol photons m^{-2} s^{-1}). However, because of continuous daylight, total daily insolation during the 2–4 months summer period is similar at low and high latitudes (*ca.* 60–80 mol photons m^{-2} d^{-1}).

In many areas of the Arctic and Antarctic, the ocean is ice-covered for most of the year. The intense attenuation of light by snow, ice, and the algal community at the base of the ice results in low irradiances at the ice-water interface and in the water column (typically less than 0.1% of irradiance at the surface of the ice; reviewed by GRENFELL and MAYKUT, 1977; MAYKUT, 1985; GRENFELL, 1991). Irradiance (I_z) at depth z below the ice-water interface can be estimated from the irradiance at the surface of the ice (I_0), and the reflective and absorptive characteristics of snow, ice, and its associated microbial community, according to:

$$I_z = I_0 \exp\{-[(k_s z_s) + (k_i z_i) + (k_m z_m) + (k_w z_w)] / \cos j\} ,$$

where k_s, k_i, k_m and k_w are the attenuation coefficients of the snow (18 to 45 m^{-1}), sea ice (0.8 to 1.5 m^{-1}), microorganisms, and seawater, respectively, z_s, z_i and z_m are the thickness of the snow, sea ice, and microbial community, respectively, and z_w is the water depth. It is assumed that only algae absorb light (absorption of light by bacteria and detritus in the ice community is negligible). Coefficient k_m can be estimated from the

concentration of chlorophyll *a* (Chl *a*) in the ice and the molar extinction coefficient for Chl *a* (0.011 to 0.035 m^2 mg^{-1} Chl *a*). Cos *j* is the fraction of the incident insolation transmitted through the sea ice. It can be approximated by:

$$\cos j = 0.5\ [1 - 0.563 \cos (2\ h_s)]\ ,$$

where h_s is the solar elevation above the horizon (in degrees) (KOZLYANINOV and PELEVIN, 1966; JERLOV, 1976). During early spring, because of the intense light attenuation by ice, snow, and algae, maximum irradiance for ice algal growth can occur at a different period than maximum I_0. In the High Arctic, maximum irradiance in the ice-algal layer generally occurs in mid-April (SMITH *et al.*, 1989, 1993), whereas the period of maximum irradiance at the surface of the ice occurs in late June. In McMurdo Sound, Antarctica, maximum irradiance for ice-algal growth is in October whereas maximum solar irradiance occurs in late December (RIVKIN, 1991). Downwelling irradiance in the water column reaches its seasonal maximum later, during the boreal or austral summer when the water is free of ice.

2.2. *Temperature*

The low water temperature, which is typical of polar marine environments, influences the structuring of habitats, the physiology of plants and animals in the biota, and the physical and flow characteristics of seawater. The effects of temperature on sea ice itself are addressed in the next section.

Temperature influences the rates of both chemical and biological reactions. Near the freezing point of seawater, the Q_{10} of most chemical and biological reactions is approximately <1.05 and 2–4, respectively. Temperature influences the kinetic energy for chemical reactions and the energy of activation, reaction rates and reaction equilibrium for biological systems (HOCHACHKA and SOMERO, 1984). The effects of temperature on the metabolic activity of marine microplankton have been extensively studied (*e.g.* LI, 1980; LI and DICKIE, 1984, 1987; WHITE *et al.*, 1991). In the temperature range of –2 to +8°C, the Q_{10} of light limited photosynthesis is typically <1.1 to 2.6 whereas the Q_{10} for light saturated photosynthesis, respiration, and growth is *ca.* 2.2 to 4.2, 2.3 to 12, and 1.4 to 2.2, respectively (TILZER *et al.*, 1986; TILZER and DUBINSKI, 1987). Thus at low seawater temperature, phytoplankton and ice algae typically have low rate of respiration, very low compensation irradiances for photosynthesis and high photosynthesis : respiration ratios (TILZER and DUBINSKI, 1987; PALMISANO *et al.*, 1985; SAKSHAUG and HOLM-HANSEN, 1986; RIVKIN and PUTT, 1987). Similarly, low temperature reduces bacterial respiration to a greater extent than growth, hence the growth efficiency of bacteria (bacterial carbon synthesized/dissolved organic carbon assimilated) in cold waters is typically higher than that observed in lower latitudes (CHRISTIAN and WEIBE, 1974; BJORNSEN, 1986; RIVKIN, unpublished). Consequently, potentially limiting nutrient resources would be used more efficiently at high than low latitudes.

Superimposed on the biological and physicochemical effects of low temperature, are at least two biophysical interactions that may influence the structure of polar food webs. Both are related to the drastic changes in dynamic viscosity near the freezing point of seawater. First, the dynamic viscosity of seawater increases rapidly with de-

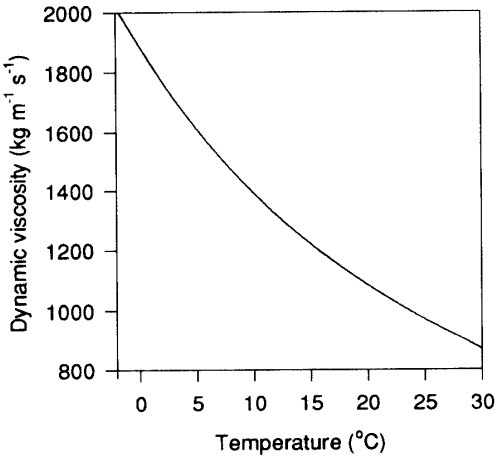

Fig. 1. Dynamic viscosity of seawater (35 psu) versus temperature, between –2 and 30°C. Values between –2 and 0°C were extrapolated. From JUMARS *et al. (1993), after* SVERDRUP *et al. (1942).*

creasing temperature so that at –2°C, it is approximately 2.5× greater than at 25°C (Fig. 1). Moreover, when viscous forces dominate, zooplankton filter feeders can influence water movement around themselves for much larger distances relative to their sizes than when turbulent forces dominate. The dominance of viscous forces may partly account, in polar regions, for (a) the relatively high clearance rates of bacterivorous flagellates and their efficient control of bacterial biomasses, (b) the reports of many large bacterivorous ciliates (GARRISON, 1991; GARRISON and GOWING, 1993), and (c) the frequent occurrence of microphagous macrozooplankton (*i.e.* organisms that can ingest particles orders of magnitude smaller than themselves). Concerning the latter point, FORTIER *et al.* (1994) report that, in polar waters of both Hemispheres, large microphages include some crustaceans (*e.g.* large copepods and Antarctic krill), which is not the case in warmer waters.

Second, the low ambient temperature in polar regions may limit diffusive fluxes of dissolved solutes across the unstirred boundary layer surrounding a cell. This could result in reduced microbial growth rates or in apparent requirement for higher nutrient concentrations (JUMARS *et al.*, 1993). Physiological or genetic adaptations to altered environmental conditions can influence nutrient acquisition by modifying the affinity of the transport system for the nutrient, thereby lowering K_m (in the Michaelis-Menten formulation), or increasing the number of absorptive sites on the cell surface, thereby increasing V_{max} (HOCHACHKA and SOMERO, 1984; MOREL *et al.*, 1991; JUMARS *et al.*, 1993). Although there is an obvious finite limit to cell size, and therefore the number of transport sites, even small changes in cell size would increase transmembrane nutrient fluxes. Clearly, the activity of transport and assimilatory systems can change with temperature, but it is not generally recognized that the diffusion coefficient is also temperature dependent. Whereas forces that drive the chemical potential are a direct linear function of temperature, the resistive forces on a solute are an inverse curvilinear function. Hence, as temperature decreases, resistive forces increase more rapidly than the decrease in forces that drive diffusion, especially at low temperatures where the temperature dependence of dynamic viscosity are greatest. The magnitude of temperature dependent changes in the diffusion coefficient appears high enough to be of ecological and biological significance (see ATKINS, 1982; OELKERS and HELGESON, 1988; OELKERS, 1991).

Although low temperature may constrain the maximum rates of biological processes, it obviously does not inhibit the development of complex trophic interactions. Indeed,

polar regions are characterized by large blooms of ice and planktonic algae, active communities of microheterotrophs, large biomasses of crustacean zooplankton, and abundant marine mammals and seabirds. As shown above, low temperature may even favor the transfer of small organic particles towards large organisms, hence improving food-web efficiency.

2.3. Seasonal ice cover

Sea ice starts forming in autumn and continues to grow throughout the winter and early spring. The presence of a seasonal ice cover reduces gas exchange between the ocean and atmosphere, which has major implications on the downward transport and potential sequestration of carbon dioxide (Section 6.2). Since sea ice does not incorporate the ions present in seawater into its crystal lattice, salts are concentrated in liquid brine during the phase of active growth. Although some of the brine is retained in ice pores, most of the very dense brine is rejected into the underlying water column where it produces thermohaline convection and deepening of the surface mixed layer (MAYKUT, 1985; LANGE *et al.*, 1989). The ratio between the liquid (*i.e.* brine) and solid phases of the developing ice as well as the connectivity of pores (and consequently the free space available for habitation) is controlled by the temperature gradient between the ice surface (which is set by air temperature) and the underlying water (temperature at the ice-water interface), which influences the rate of ice growth. The colder the ice, the more brine it retains when it freezes. Organisms inhabiting the upper region of the ice need to be both halotolerant and psychrophilic (GARRISON and BUCK, 1991; STOECKER *et al.*, 1992; PALMISANO and GARRISON, 1993). In newly formed ice, most of the volume is occupied by small brine channels (*e.g.* 10 μm to 1mm). As the ice ages, thickens, and cools, the brine drains and the channels enlarge (from several millimetres to tens of centimetres) providing habitats, during the period of seasonally low solar radiation, for an heterotrophic community which comprises bacteria, protozoa and small animals.

In spring, microalgae occupy the solid substratum provided by the ice matrix. When solar irradiance exceeds the compensation intensity for growth, algae can accumulate to very high biomasses, especially in the ice bottom (*e.g.* HORNER *et al.*, 1992). The total attenuation of incident solar radiation by the snow and ice cover and the ice algae is frequently so high that submarine irradiance is severely reduced, especially during the ice-algal bloom. As a result, phytoplankton production in the under-ice water column is generally quite low. As the ice warms, the channels narrow, eventually to strings of sub-millimetre pores at *ca.* –5°C. Porosity of the ice and the connectivity and size of the pores change with temperature (PEROVICH and GOW, 1991). The progressive change in the temperature-dependent pore size contributes to the structuring of the sea ice community in at least two ways (EICKEN, 1992). First, it determines the trophic relationships within the ice by providing refuges for small grazers, such as protozoa, which have access to the sub-millimetre pores whilst large grazers, such as copepods and amphipods are restricted to larger, millimetre to decimetre channels. Second, it influences the development and progression of communities by controlling exchanges of nutrients between the ice and the underlying water (CLARKE and ACKLEY, 1984; REEBURGH, 1984; COTA *et al.*, 1987; GARRISON *et al.*, 1990). In the ice bottom, absorption of solar radiation by the dense layer of algae can favor degradation of the ice matrix, and result in local

melting while air temperature is still well below freezing.

Later in the season, as the desalinated ice melts, the freshening of the surface layer vertically stabilizes the upper water column. The reduction of the ice cover has two effects: it increases stratification and decreases the attenuation of light so that irradiance in the water column is higher. The combined effect of these two factors, given that nutrients in the surface mixed layer are then normally abundant, is to stimulate the growth of phytoplankton (critical depth model; SVERDRUP, 1953). Since there generally is a time lag between enhanced phytoplankton production and grazing by mesozooplankton, a bloom often accompanies retreating ice edges (*e.g.* SCHANDELMEIER and ALEXANDER, 1981; SAKSHAUG and HOLM-HANSEN, 1984; NIEBAUER and ALEXANDER, 1985; SMITH, 1987).

3. Environmental Characteristics of Arctic Ocean Continental Shelves

3.1. Riverine inputs

The overall situation in the Arctic Ocean has been summarized as follows by MACDONALD *et al.* (1989): "The Arctic Ocean can be considered as a large, complex estuary where seasonal runoff impinges on wide shelves synchronously around the basin edge; in fact, the combined inflow (about 3500 km^3 yr^{-1} [TRESHNIKOV, 1985]) is surpassed in magnitude by only the Amazon. Additional runoff (estimated at 1670 km^3 yr^{-1}) [...] enters indirectly through the Bering Strait. Unique to cold region estuaries is a melt-freeze cycle which can cause positive or negative estuarine forcing [CARMACK *et al.*, 1989]."

The riverine flow and input of low salinity water through the Bering Strait contributes significantly to the strong halocline (Section 3.3) and generally shallow surface mixed layer throughout most of the Arctic Ocean. The total annual riverine input into the Arctic Ocean occurs mainly in summer (CARMACK, 1990). Average annual surface salinity variations on the shelves is 2–4 psu compared to 0.5 psu offshore (COACHMAN and AAGAARD, 1974; CARMACK, 1990). Although the hydrographic and flow characteristics of individual rivers vary, low salinity river water generally spreads as a buoyant plume under the sea ice. In spring and summer, because of the high river flow, shelf waters are diluted and the shelves act as a positive estuary with a net outflow of low density water at the surface. In winter, due to the production of brine during sea ice formation in the nearshore, salinities on the shelf can be highest (AAGAARD *et al.*, 1981; MELLING and LEWIS, 1982) and the shelves are a reverse estuary with a net outflow of higher density water at depth. The formation of dense brines may have a significant effect on the benthic-pelagic nutrient dynamics (Section 3.2).

Riverine inputs of inorganic and organic nutrients may be important in determining the cycles of production, and hence the structure of food webs on the Arctic continental shelves. For example, the average concentrations of several biologically important nutrients in the plumes of major Canadian and Siberian rivers flowing onto the shelf are very high, *i.e.* 8–12 mg l^{-1} of total organic carbon (TOC) of which about half is dissolved (DOC) and half is particulate (POC), 0.2 to 0.4 mg l^{-1} of dissolved organic nitrogen (DON), and 0.1 to 0.2 mg l^{-1} of dissolved inorganic nitrogen, mainly NO_3, NO_2 and NH_4 (TELANG *et al.*, 1991). Thus, significant quantities of allochtonous organic matter are transported into the nearshore. Over half of the annual sedimentation of carbon on the

shelves comes from terrigenous sources, primarily very old peat, the remainder being of ice and planktonic algal origins. Stable isotope studies have shown that amphipods on the bottom can directly ingest the terrigenous carbon (SCHELL 1983; SCHELL *et al.*, 1989) and act as a link towards some apex predators (Section 6). Although animals other than amphipods do not appear to consume allochtonous POC, the fact that it does not accumulate to a substantial amount suggests the importance of nearshore processes such as microbial decomposition and nutrient remineralization, both in the water column and on the bottom.

3.2. Bottom processes

On the Arctic continental shelves, high salinity brine resulting from ice formation sinks to the bottom. This produces high salinities (>36 psu) and densities near the bottom, over large areas of the shelf (NEWBURY, 1986; MACDONALD and THOMAS, 1991). The high-density bottom water could displace nutrient-enriched sediment pore water with the low nutrient brines. These conditions would be appropriate for extracting mobilized substances from the sediments. The rates and patterns of regeneration of DOC and DON have not been studied on Arctic continental shelves. However, high regeneration rates for NO_3 and PO_4 from the sediments of the Arctic shelf have been determined (ANDERSON *et al.*, 1988).

Nutrients extracted from nutrient-enriched pore water are either transported across the shelf in the slow thermohaline circulation or vertically mixed back into the shallow water column (MELLING and LEWIS, 1982; MACDONALD and THOMAS, 1991). Nutrients advected across the shelf, into the Arctic Ocean basins, contribute significantly (*ca.* 10% of the standing stock) to the inorganic nutrient maximum in the upper halocline (Section 3.3), over extensive regions of the Arctic Ocean (JONES and ANDERSON, 1986, 1990; ANDERSON *et al.*, 1988).

3.3. Shelf-basin exchange: the permanent halocline

The central basins of the Arctic Ocean are almost continuously ice covered. There, the vertical structure of the water column is characterized by a low salinity surface layer, which is separated from deeper Atlantic waters by a pronounced halocline and associated nutrient maximum (JONES and ANDERSON, 1986, 1990); under the Atlantic layer is the Arctic Ocean Deep Water. At a station near 85°45′N, 111°E (station CESAR; ANDERSON *et al.*, 1990), characteristics of the various layers were as follows: surface (0–55 m, <–1.5°C, 30 to 32 psu), halocline (55–350 m, –1.5 to 0.4°C, 32 to 34.8 psu), Atlantic (350–750 m, 0.4 to 0.5°C, 34.9 psu), Arctic Deep (>750 m, –0.5 to 0.4°C, 35.0 psu). The halocline is favored by the permanent ice cover, which inhibits mixing by wind.

The permanent halocline is a distinctive feature of central Arctic basins. The two mechanisms proposed by AAGAARD *et al.* (1981) to explain this structure have received support from later studies, *i.e.* ice formation during winter on shelves (MOORE *et al.*, 1983; JONES and ANDERSON, 1986) and upwelling and cooling of Atlantic water (STEELE *et al.*, 1995), so that the two may play a role. The relatively low salinity of the cold, shallow surface mixed layer is caused by seasonal river runoff and melting of sea ice on shelves. The main source of the cold saline water in the halocline is thought to be the continental shelves, where dense water is formed at the time of freezing, after which it

would flow towards the central basins. Because polynyas on Arctic Ocean shelves produce brine during several months every year, these often play a major role in exporting water and chemicals from the shelves to the central basins (*e.g.* MARTIN and CAVALIERI, 1989). Overall, freshwater inputs from rivers and sea ice melting maintain the low salinity of the Arctic surface layer, while the formation of brine on the shelves contributes to the ventilation of the halocline (AAGAARD *et al.*, 1981; MELLING and LEWIS, 1982).

4. General Characteristics of Pelagic Marine Ecosystems

Pelagic marine ecosystems may be seen as a web of interconnected pathways, through which dissolved inorganic carbon (DIC, *i.e.* CO_2, which is present in seawater as free CO_2 and derived chemical species) and dissolved organic carbon (DOC) are incorporated into living organisms and channeled towards pools of biogenic carbon with different turnover times (*i.e.* time elapsed between the transformation by photosynthesis of DIC into POC and DOC and the subsequent oxidation to CO_2 and release into the surface waters or atmosphere). LEGENDRE and LE FÈVRE (1992) proposed three pools, *i.e.* short-lived organic carbon ($<10^{-2}$ years), long-lived organic carbon (10^{-2} to 10^{2} years) and sequestered biogenic carbon ($>10^{2}$ years). Short-lived organic carbon consists of organisms with high turnover rates and labile dissolved organic compounds. Long-lived organic carbon includes large animals, such as fish and marine mammals and birds. Sequestered biogenic carbon comprises organic remains buried in sediments (including petroleum), inorganic deposits of biological origin (*e.g.* calcareous ooze, coral reefs, continental limestone), refractory dissolved organic matter, and dissolved CO_2 in deep waters resulting from the oxidation of organic compounds (respiration). Climate changes at various time scales (*e.g.* glaciations, interglacial oscillations, and the possible ongoing global warming) may be related to (or mediated by) variations in the pool of sequestered carbon.

The primary source of organic carbon in the biosphere is photosynthesis, the process through which the free energy of sunlight is converted to chemically bound energy, which is used to synthesize organic carbon from DIC, water, and inorganic nutrients. Organic matter synthesized by algae is transferred to the different pools of biogenic carbon through a number of trophic pathways. The basic principle governing transfer is that organisms normally feed on particles smaller than themselves. In oceans, it has been estimated that the average size ratio between pelagic organisms and their food particles is *ca.* 14 (SHELDON *et al.*, 1977).

Except in shallow waters where seaweeds can grow attached to the bottom, most marine primary producers are microscopic algae (phytoplankton) that float in the upper water column, where solar irradiance is high enough for photosynthesis to take place (euphotic zone). Sizes of phytoplankters cover almost four orders of magnitude, from *ca.* 2000 μm (diatom *Ethmodiscus rex*, in warm oceanic waters) to 0.6–0.7 μm (ubiquitous prochlorophytes). In addition, photosynthetic products include organic matter exuded by phytoplankton. In a functional sense, the size range should include the dissolved organic matter released by phytoplankton during photosynthesis. Although marine microbiologists normally separate bacterioplankton from seawater using a 0.2 μm filter, thus considering that the <0.2 μm filtrate contains only dissolved compounds, this

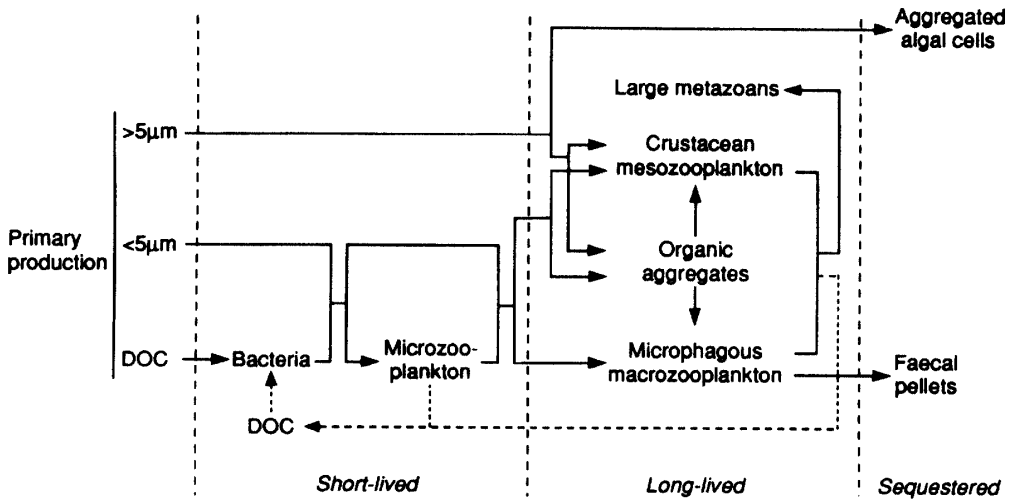

Fig. 2. Major trophic pathways in marine waters (full arrows), from the three size classes of primary production (i.e. cells >5 μm, cells <5 μm, and dissolved organic carbon) to the three pools of biogenic carbon (i.e. short-lived, long-lived, and sequestered), and food-web recycling of DOC (dashed arrows), from consumers to heterotrophic bacteria. Modified from LEGENDRE *(1996).*

fraction actually includes colloidal material and free viruses (0.1 μm). Given that the size spectrum of photosynthetic products is continuous, from the largest phytoplankton to the smallest exuded organic molecules, size limits between the large and the small phytoplankton and DOC are somewhat arbitrary. The same is true for the turnover times of biogenic carbon, whose spectrum is also continuous.

Given the wide size range in the forms of primary production (*i.e.* from DOC to *ca.* 2000 μm algae), there is a correspondingly wide size range of consumers (Fig. 2). Dissolved organic matter is assimilated and used for both anabolic and catabolic reactions by free-living heterotrophic bacteria (*ca.* 1 μm) and perhaps some heterotrophic flagellates (TRANVIK *et al.*, 1993; TRANVIK, 1994). Small phytoplankton (<2 or 5 μm; include small eucaryotes and procaryotic cyanobacteria and prochlorophytes) are grazed primarily by protozoa (nanozooplankton, 2–20 μm; microzooplankton, 20–200 μm). Hence, the oxidation of DOC by heterotrophic bacteria and from respiration by small organisms may shorten the turnover time of organic carbon. Large phytoplankton (>2 or 5 μm) are grazed by a variety of mesozooplankton (200–2000 μm; mainly crustaceans). In addition, some large zooplankton (from *ca.* 10 to >100 mm; *e.g.* salps, pteropods, doliolids, and appendicularians and also some large crustaceans in polar waters) have the ability to feed directly on particles ≤5 μm, which are 10^3 to 10^4 times smaller than themselves (FORTIER *et al.*, 1994). The flux of organic carbon into the long-lived pool is mediated by mesozooplankton (mainly copepods) grazing on large cells, organic aggregates (*e.g.* marine snow), and microzooplankton and by microphagous macrozooplankton feeding on small particles and aggregates. Part of this flux reaches large animals such as fish, marine mammals and birds. Finally, sedimentation to deep water of rapidly sinking aggregated algal cells and faecal pellets (mainly from microphagous macrozooplankton) may lead to the sequestration of biogenic carbon in deep ocean basins and, to a smaller extent, in sediments on continental shelves.

The various modes of consumption of photosynthetic production lead to different trophic pathways. (1) Grazing on large phytoplankton by mesozooplankton, which are themselves prey to larger organisms, is called herbivorous food chain or web. (2) At the other end of the size spectrum is the microbial loop, in which heterotrophic bacteria are grazed primarily by flagellates, which are in turn prey to ciliates. Flagellated and ciliated protozoa regenerate dissolved organic compounds, which are used by bacteria. The microbial loop obviously cannot go on indefinitely, because organic carbon is mineralized (*i.e.* respired to CO_2) by all organisms involved, so that maintenance of the loop requires an external source of DOC. This source may be allochthonous, as for example on Arctic Ocean shelves where river runoff transports large amounts of organic and inorganic nutrients from continents (see Section 3.1), or it may be autochthonous (local primary production). When solar irradiance is too low to allow photosynthesis, the water column is, by necessity, dominated by the microbial loop. However, in cases where the input of allochthonous DOC is relatively high, there could be export of carbon from heterotrophic bacteria to larger organisms via bacterial based food webs (*e.g.* mesozooplankton preying on protozoa, which are feeding on bacteria), so that the loop would no longer be closed. (3) When solar irradiance permits photosynthesis, the resulting trophic pathway is called microbial food web (in the literature, the terms microbial loop and microbial food web are often confused; see RASSOULZADEGAN, 1993). In the latter, small phytoplankton, in addition to heterotrophic bacteria, are grazed by flagellated and ciliated protozoa, which in turn remineralize dissolved inorganic and organic nutrients, that are used by small phytoplankton and bacteria. Since there is an input of primary production, the microbial food web can export biogenic carbon to larger organisms via mesozooplankton feeding on microzooplankton. The ultimate source of autochthonous DOC for bacterial production is phytoplankton production, but actual production of DOC involves, in addition to exudation, phytoplankton spontaneous autolysis, viral lysis, excretion by herbivores, sloppy feeding of large zooplankton and degradation of faecal material and other detritus (see KIRCHMAN *et al.*, 1993). (4) Although the herbivorous and microbial trophic modes are often perceived as exclusive of each other, LEGENDRE and RASSOULZADEGAN (1995) proposed that there are systems where the two trophic modes are concurrent. This trophic configuration, called multivorous food web, can be significant in polar regions. (5) Finally, large microphages grazing on small particles effectively transfers biogenic carbon directly from small plankton to large pelagic grazers. FORTIER *et al.* (1994) have shown that large microphages are especially efficient at channeling part of the biogenic carbon that would have otherwise been shorter lived towards the long-lived (*e.g.* fish, marine mammals and birds) and even sequestered carbon pools. In the present paper, the term "export" covers the channeling of primary production out of the euphotic zone to both large animals and deep waters.

Copepods are the most abundant mesozooplankton in oceans. Herbivorous copepods generally link the production of large phytoplankton to that of fish and, until recently, it was generally accepted that the herbivorous chain from large phytoplankton to copepods and to fish was underlying all important fisheries (*e.g.* RYTHER, 1969; CUSHING, 1989). However, there is growing evidence that many copepods can switch from feeding on phytoplankton to microzooplankton, thus allowing exploitation of both the herbivorous and the microbial food webs (*e.g.* GIFFORD and DAGG, 1991; PIERCE and TURNER,

1992; OHMAN and RUNGE, 1994). This new perspective should eventually result in a revision of present models, which predict the export of biogenic carbon from local primary production.

5. Ecosystem Characteristics of Arctic Ocean Continental Shelves

5.1. Production and sedimentation of algae

In the Arctic Ocean, ice algae account for about 25% of the total primary production of 2.8×10^{14} g C year^{-1} (20 g C m^{-2} year^{-1}; LEGENDRE *et al.*, 1992). Most of the Arctic annual ice algal production of 70×10^{12} g C is accounted for by algae growing in the first-year ice, which occurs primarily over the continental shelf. In multi-year ice, which occurs primarily over the central basins of the Arctic Ocean, primary production is thought to be very low because of the low transparency and high light attenuation characteristics of this ice. In the water column under first-year ice, during spring, the very low irradiance and lack of stratification results in dominance by small phytoplankton (*e.g.* ROBINEAU *et al.*, 1994).

The ice algal community is dominated by large unicellular algae, mostly diatoms (HORNER *et al.*, 1992). Blooms at ice edges and in open shelf waters are also often dominated by large diatoms (SMITH and NELSON, 1985; SMITH, 1987). Diatoms have relatively high sinking rates (1–10 m d^{-1}; SMAYDA, 1970). Ice algae may be released as a pulse (HORNER and SCHRADER, 1982; TREMBLAY *et al.*, 1989; MICHEL *et al.*, 1996) and part of the algal biomass may reach the benthos (CAREY, 1987) or be consumed by pelagic grazers (TREMBLAY *et al.*, 1989; MICHEL *et al.*, 1996). The residence time of ice algal cells in the suspended biomass, after their release from the ice, is shorter in shallow than in deep waters, so that a larger proportion of the sinking algae may reach the benthos. Indeed, significant export of ice algae to the benthos has been observed in shallow Beaufort (CAREY, 1987) and Chukchi Sea (MATHEKE and HORNER, 1974). In deeper waters, transfer of algae to pelagic grazers is favored by the long residence time of cells in the water column. It follows that the relative contributions of intact algae and faecal pellets to the vertical flux of organic matter should vary depending on water depth and thus generally exhibit an inshore-offshore gradient. Moreover, where the water column is sufficiently deep, coprophagy, coprorhexy, and bacterial mediated remineralization of faecal pellets would alter the size structure and chemical composition of the sinking flux. Hence, the nutritional quality of the sinking material will likely decrease in the offshore direction. However, the fate of primary producers will also depend on the timing of zooplankton grazing relative to primary production and the type and abundance of grazers (PEINERT *et al.*, 1989; WASSMANN and SLAGSTAD, 1993).

Sedimentation to the bottom of large quantities of organic material leads to the development of large and productive epibenthic populations in nearshore regions, and of a less productive benthic community offshore (ALTON, 1974; CAREY *et al.*, 1984a, b; DAYTON, 1990). The inshore to offshore gradient in benthic productivity may parallel the sedimentation delivery of high quality biogenic material in the form of algal biomass and herbivorous faecal pellets, which is superimposed on large allochtonous input of organic matter in the nearshore (Section 3.1).

5.2. Zooplankton grazing

The dominant mesozooplankton copepods on Arctic shelves are *Calanus hyperboreus*, *C. glacialis*, *C. finmarchicus*, *Metridia longa*, *Pseudocalanus* spp., *Acartia longiremis*, *Euchaeta* spp. and *Oithona similis* (CONOVER and HUNTLEY, 1991). Although all feed in the plankton, *C. hyperboreus*, *C. glacialis* and *Pseudocalanus* spp. can also feed on ice algae (CONOVER *et al.*, 1986; RUNGE and INGRAM, 1988; MELNIKOV, 1989a). *Metridia longa*, *A. longiremis* and *Oithona similis* are omnivorous and ingest phytoplankton, zooplankton eggs, and other non-chlorophyllous prey such as flagellated and ciliated protozoans. Moreover, recent evidence indicates that *O. similis* is coprophagous which, depending upon their abundance and prey availability, may influence the downward flux of biogenic carbon (GONZÁLEZ and SMETACEK, 1994; GONZÁLEZ *et al.*, 1994).

Except during the period that follows the release of algae from the ice and during phytoplankton blooms, the algal community in the water column is dominated by small cells, which are below the size threshold (*ca.* 5 μm; FORTIER *et al.*, 1994) that pelagic grazers such as copepods can effectively ingest. The only large zooplankton able to exploit small algae are some pelagic microphages, such as pteropods, tunicates and, in northern waters, a few large copepods (*e.g. Neocalanus*, *Eucalanus*; FORTIER *et al.*, 1994). Under these conditions, when the food supply is potentially limiting, copepods could switch from herbivory to omnivory and ingest microbial food web components such as protozooplankton.

Direct measurements of ingestion of microzooplankton by copepods in the Arctic are lacking. However a large number of studies from temperate oceans (GIFFORD, 1991; GIFFORD and DAGG, 1991; LANDRY *et al.*, 1993; SANDERS and WICKHAM, 1993 and references cited therein) and seasonally cold coastal waters (OHMAN and RUNGE, 1994) have clearly shown that copepods can be omnivorous and ingest non-chlorophyllous prey, of the appropriate size, such as protozoan flagellates and ciliates. For example, during open water periods (June–July) in the Gulf of St. Lawrence, *Calanus finmarchicus* sustains high rates of egg production by ingesting microzooplankton despite low Chl *a* concentrations (OHMAN and RUNGE, 1994). Indeed, microzooplankton might be a better food source than phytoplankton for mesozooplankton (*e.g.* CORNER *et al.*, 1976). *Calanus finmarchicus* is abundant in the Gulf of St. Lawrence during April, under ice cover and at temperature <-1°C, and in the Arctic (CONOVER and HUNTLEY, 1991). Thus, it is likely that omnivory on protozoa is common among Arctic shelf copepods, when phytoplankton of the appropriate size are scarce or during periods when submarine irradiances are too low to support primary production.

Ciliated and flagellated microzooplankton ingest small prey such as heterotrophic bacteria and small algae, when the latter are present (AZAM *et al.*, 1983; LEGENDRE and RASSOULZADEGAN, 1995). Small autotrophs originate from the ice-bottom community or from autochthonous growth in the water column. Although large populations of bacteria can develop in the ice bottom, their areal biomass is smaller than in the water column (MARANGER *et al.*, 1994). Furthermore, due to their small size and negligible sinking rates, sea-ice bacteria generally do not contribute to the sinking flux of biogenic carbon, except perhaps when they are attached to large particles such as ice algae (GROSSI *et al.*, 1984; SULLIVAN and PALMISANO, 1984; SMITH *et al.*, 1989; GROSSMANN and GLEITZ, 1993). Thus, bacterivorous microzooplankton would primarily ingest planktonic bacteria. There

are three primary sources of dissolved substrates for bacterioplankton growth: (1) autochthonous regeneration within the water column, (2) benthic regeneration followed by upward mixing into the water column, and (3) allochthonous inputs from rivers. All three sources may be important in nearshore shelf environments. As noted in Section 3.1, the riverine inputs of DOM and POM are large and may be a regionally important source of substrate for bacterioplankton. However riverine inputs of dissolved nutrient are diluted by the time they reach the outer shelf, hence microheterotrophic production there should be sustained primarily by autochthonous water column and benthic regeneration.

5.3. Seasonal patterns of trophodynamics

Because of the seasonal cycle in solar irradiance, the water column on Arctic Ocean shelves is necessarily dominated by heterotrophy during at least half the year, when irradiance is too low to sustain photosynthesis, and by autotrophy during the remainder, when photosynthesis becomes high enough to allow growth of microalgae in the ice and the water column. For simplicity (Fig. 3), the seasonal cycle is divided here in three seasons, *i.e.* autumn–winter (low or null solar irradiance), spring (high solar irradiance

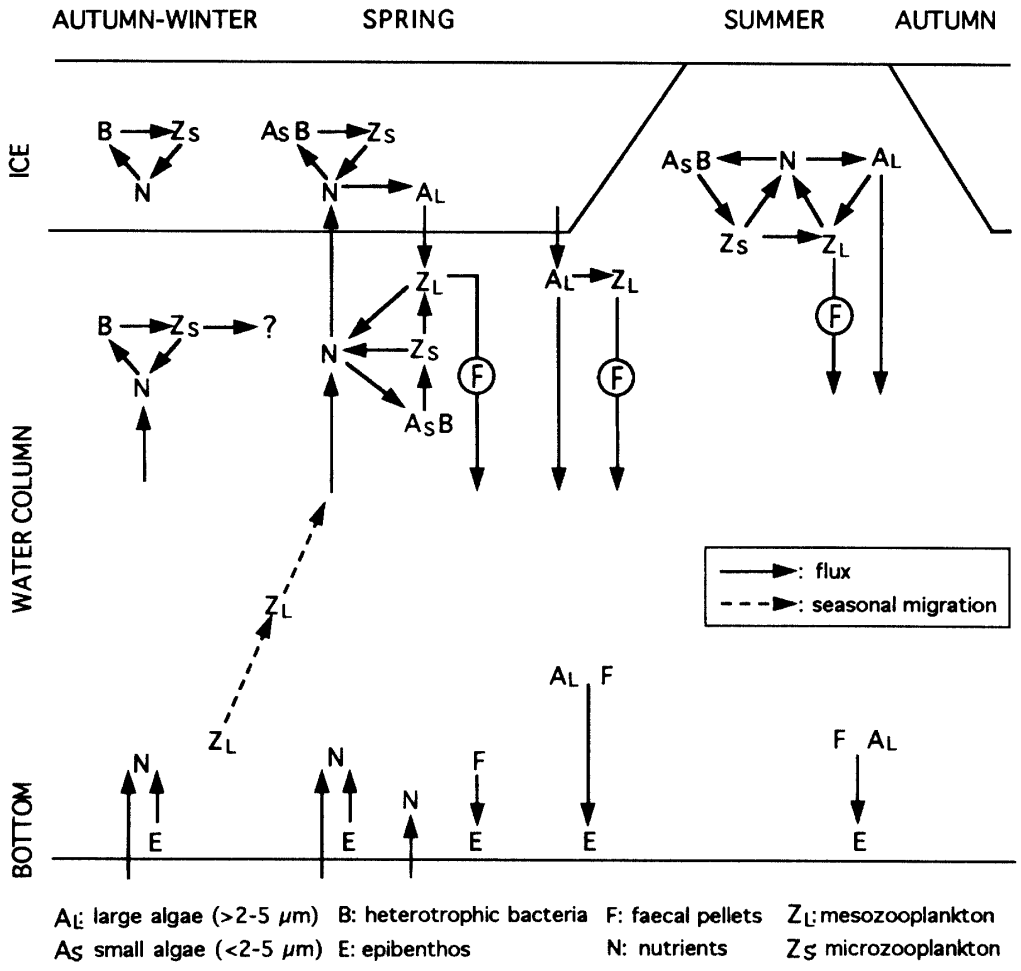

Fig. 3. Seasonally changing interactions among trophic components of the marine food web, within and between ice, water column and bottom sediments.

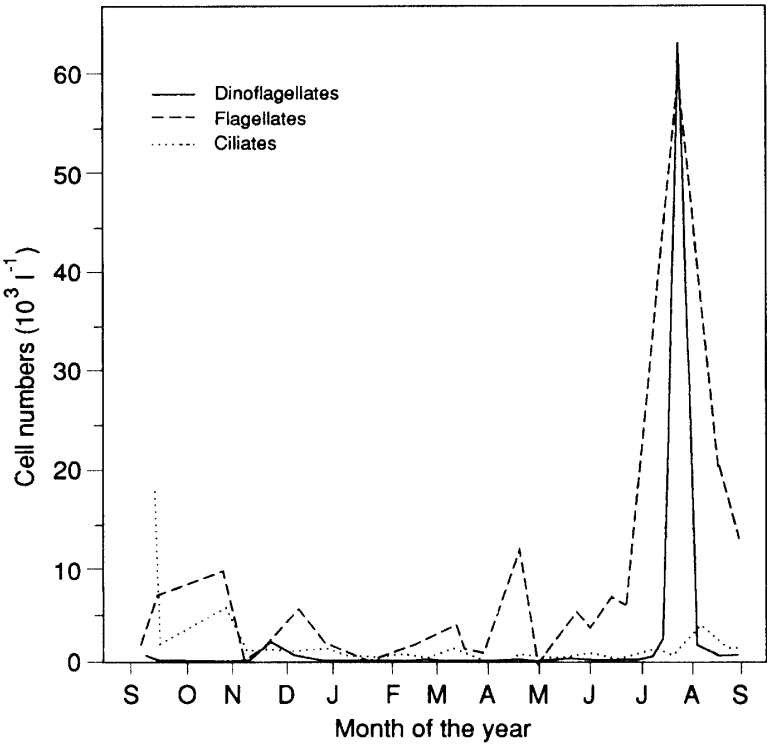

Fig. 4. Seasonal variations in abundances of planktonic flagellates, dinoflagellates and ciliates at Igloolik, Canadian Arctic. Adapted from BURSA *(1961).*

and ice cover), and summer (high solar irradiance and open water). The transition between spring and summer corresponds to the period of snow and ice melt. Also for simplicity, the system is divided on the vertical in three compartments, *i.e.* the ice, the water column (under ice cover or ice free), and the bottom sediments. Figure 3 summarizes, for each season, interactions among trophic components of the marine food web, within and between compartments. Only a few trophic components are considered here, *i.e.* nutrients, large and small algae, heterotrophic bacteria, large and small zooplankton, and epibenthos. Transfers from large zooplankton and benthos to Arctic cod and apex predators are examined in Section 6.1.

During autumn and winter, irradiance is generally too low to sustain primary production and large zooplankton are mostly in diapause in deep waters (CONOVER and HUNTLEY, 1991). Thus, trophic activity in the ice and the water column should be restricted to the microbial loop. There is regeneration in bottom sediments and release in overlying waters of inorganic and organic nutrients (Section 2.2), of which some are expected to be mixed upwards by eddy diffusion (*e.g.* dissipation of tidal energy). Because organic nutrients can sustain the production of heterotrophic bacteria, it can be hypothesized that, in the ice and the water column, bacteria are grazed by small zooplankton, which in turn release nutrients that are used by bacteria, hence a microbial loop. BURSA (1961) described the annual plankton cycle in the Canadian Arctic (Fig. 4). He reported the presence of flagellates during the whole winter and peak abundances of flagellates and dinoflagellates in August and of ciliates in September (Fig. 4). Continu-

ous occurrence of flagellates is indicative of the presence of an active microbial loop under Arctic sea ice during winter. BURSA (1961) also reported preponderance of holozoic over autotrophic dinoflagellates, which he interpreted as a common phenomenon in the Arctic environment given the long period of darkness and low temperature. In the Southern Ocean, bacterial production may be important for overwintering krill (MARCHANT and NASH, 1986; MARCHANT, 1990). In the Arctic, the fate of the hypothesized winter microbial production is presently unknown, hence the question mark in Fig. 3.

In spring, as solar irradiance increases, autotrophic production superimposes itself on the winter microbial loop, leading to microbial and herbivorous food webs. Production of small algae, in the ice bottom and the water column, adds to the food available to small zooplankton, thus accelerating microbial food web activity. Because small autotrophs, in addition to heterotrophic bacteria, are available to microzooplankton, the system is no longer closed so that the microbial food web can export carbon to mesozooplankton, especially in the water column. Grazing by large and small zooplankton regenerates nutrients that sustain algal and bacterial production. Production of diatoms in the ice can result in a large accumulation of biomass and, depending on the tidal energy and rate of nutrient replenishment, the local availability of nutrients can limit algal growth when biomass is high (GOSSELIN *et al.*, 1990). It follows that the maximum yield of algal biomass in bottom ice may be controlled by nutrient replenishment from the underlying water column (MAESTRINI *et al.*, 1986; COTA *et al.*, 1987). A variable proportion of the large algae in the ice can be grazed by large zooplankton. Vertical migrations of copepods to the undersurface of the ice (CONOVER *et al.*, 1986; RUNGE and INGRAM, 1988, 1991), and the presence of diatoms in the guts and faeces (BRADSTREET and CROSS, 1982; RUNGE and INGRAM, 1988) indicate that copepods graze on ice algae. It has been shown that this early feeding on ice algae may play an important role in Arctic food webs, in providing female copepods with the food required to complete sexual maturation and thus produce eggs early enough that nauplii can take advantage of the phytoplankton bloom in the water column, a few weeks later (RUNGE *et al.*, 1991).

In late spring or early summer, the algal material accumulated in seasonal ice is released in the water column. According to environmental conditions, algae released from the ice may either rapidly sink to the bottom, as aggregates of intact cells, or remain in suspension for a few days to a few weeks, and be thus available to grazing by large zooplankton (Section 5.1).

In summer, following ice melt or break-up, there is often a bloom of large phytoplankton in open waters, of which part is grazed in the water column by large zooplankton and part sinks as intact cells or in faecal pellets (HSIAO, 1987; HARGRAVE *et al.*, 1989; WASSMANN *et al.*, 1990). At late successional stages of the bloom, bacterial colonization of organic matter can also occur, as evidenced for senescent colonies of *Phaocystis pouchetii* (THINGSTAD and MARTINUSSEN, 1991). This would influence the carbon budget in the upper water column and the availability of material for later sedimentation. Moreover, increased abundance of microzooplankton at the end of summer (Fig. 4) suggests that large zooplankton can switch from herbivory to omnivory after the phytoplankton bloom (GRAINGER, 1959; BURSA, 1961). On the bottom, sedimented algal material is used by the benthic fauna, first by epibenthic suspension feeders and then by the remainder of the benthic food web, leading to regeneration of nutrients and, in some cases, burial of

part of the organic matter in sediments (DAYTON, 1990).

6. Export and Sequestration of Biogenic Carbon

6.1. Export to apex predators

In the Arctic Ocean, apex predators include polar bear (*Ursus maritimus*), baleen whales (Mysticetes; bowhead; *Balaena mysticetus*, fin whale; *Balaenoptera physalus*, gray whale, *Esrichtius robustus*), toothed whales (Odontocetes; narwhal, *Monodon monoceros*; white whale, *Delphinapterus leucas*), seals (Phocidae; bearded seal, *Erignathus barbatus*; harp seal, *Phagophilus groenlandicus*; ribbon seal, *Histriophoca fasciata*; ringed seal, *Phoca hispida*), fur seal (Otariidae; *Callorhinus ursinus*), walrus (Odobenidae; *Odobenus rosmarus*) and seabirds of several families. The subject has been recently reviewed by AINLEY and DEMASTER (1990). The most important habitat feature of polar regions for apex predators is sea ice and, according to these authors, the main effects of ice in the north polar regions are negative, *i.e.* the presence of sea ice prevents access to the water, and therefore to the main source of food for many of the predators (*e.g.* bears, seals, walruses and seabirds), and it reduces submarine irradiances, hence, low primary production.

An alternative view is that sea ice both extends the foraging range for quadrapedal predators such as the polar bear and provides a refuge from predation for some species. For example, pressure ridges provide opportunities for snow accumulation to depths sufficient for construction of birth lairs by seals. These lairs hide and protect neonates from predators such as polar bears and arctic fox (HAMMILL and SMITH, 1989; SMITH and LYDERSEN, 1991). Concerning the low under-ice irradiance, annual primary production in seasonally ice-covered waters is quite similar in the Arctic and Antarctic (*ca.* 20 and 10 g C m^{-2} $year^{-1}$, respectively; LEGENDRE *et al.*, 1992). The fact that the two regions support large populations of apex predators indicates that primary production, although not very high, is efficiently channeled toward these organisms. An important characteristic of the Arctic Ocean in this respect is the extensive system of shallow shelves, which permits many apex predators to feed on benthos. Another potentially significant characteristic is the low water temperature, which favors efficient fluxes from small producers towards large grazers.

On Arctic Ocean shelves, an important part of the diet of apex predators is supplied by benthic organisms, either directly or through Arctic cod (*Boreogadus saida*). Arctic cod is the key species that links primary production to apex predators. This fish is an important component of the diet of most apex predators and it is also preyed upon by animals that are part of the diet of these predators (*e.g.* squids, which are eaten by narwhals and white whales in addition to Arctic cod; ringed seals, which are eaten by polar bears). Arctic cod feed on a variety of pelagic crustaceans and benthic organisms (*e.g.* BRADSTREET and CROSS, 1982), that are themselves also part of the diet of apex predators. There are a few apex predators which do not use Arctic cod as food, directly or indirectly (*e.g.* walruses eat mostly bivalves; some birds feed on small planktonic or benthic crustaceans). Sculpins (*e.g. Gymnelus viridis*, *Icelus bicornis*, *Triglops pingeli*) are also common on continental shelves in the Arctic (GREEN and STEELE, 1977) and adjacent seas (*e.g.* Hudson Bay; MORIN and DODSON, 1986). Sculpins consume amphi-

pods (MORIN and DODSON, 1986) and could therefore contribute to the transfer to apex predators of allochtonous carbon entering nearshore waters. For example, white whales feed on a variety of benthic organisms, including sculpins (SERGEANT, 1962).

DAVIS *et al.* (1980) summarized the major trophic pathways leading to marine mammals in the North American Arctic, distinguishing between nearshore and offshore waters. Their scheme was modified and expanded (BRADSTREET and CROSS, 1982; BRADSTREET *et al.*, 1986) and used as a basis by AINLEY and DEMASTER (1990) for their model of trophic pathways leading to apex predators in coastal and offshore waters in the high Arctic. The basic difference between coastal and offshore waters is that benthic resources play a much more important role in the nearshore than the offshore, in both the direct feeding of apex predators and the diet of Arctic cod. During the ice-covered season, polynyas permit access to open water, and they are often the site of high water-column primary production (*e.g.* up to 2700 mg C m^{-2} d^{-1}, in the Northeast Water Polynya; PESANT *et al.*, 1996.) Consequently, polynyas are focal areas for active foraging by apex predators and, hence, traditional hunting areas for native people (DUNBAR, 1981).

6.2. *Export to deep waters and sequestration*

YAGER *et al.* (1995) recently proposed a model for the potential sequestration of biogenic carbon in seasonally ice-covered waters. Their "rectification hypothesis" was developed for the annual carbon cycle in polynyas, but it applies to any seasonally ice-covered waters. As summarized in LEGENDRE (1996), the hypothesis (Table 1) considers two broad pools of carbon in oceans, *i.e.* total inorganic carbon (C_T) and organic carbon (OC), and fluxes between the atmosphere (AT), the surface waters (SW) and the deep waters (DW). During the ice-free summer period, phytoplankton production in the SW transfers carbon from the inorganic pool to the organic pool ($C_T \rightarrow OC$) and there is sink-

Table 1. Annual cycle of biological and physical processes affecting the cycling of CO_2 in regions with seasonal sea ice, i.e. "rectification" hypothesis of YAGER et al. (1995). Two pools of carbon in oceans are considered: total inorganic carbon (C_T) and organic carbon (OC). Fluxes are between the atmosphere (AT), the surface waters (SW) and the deep waters (DW). Modified from Fig. 6 of YAGER et al. (1995) by LEGENDRE (1996).

Season	Dominant processes	Carbon pools	Carbon fluxes
Summer	Phytoplankton production	$C_T \rightarrow OC$	OC: SW→DW
Early autumn	Invasion of atmospheric CO_2 in surface waters and deep vertical mixing	$C_T \leftrightarrow OC$	CO_2: AT→SW OC: SW→DW C_T: DW→SW
Late autumn and winter	Respiration > primary production	$OC \rightarrow C_T$	None: ice acts as barrier
Spring - Before ice melts - Ice melt	Ice algal production Near-surface stratification	$C_T \rightarrow OC$	None: ice acts as barrier Stratification acts as barrier OC: SW→DW

NOTE: At no time during the seasonal cycle is there a flux such that C_T: SW→A. Hence potential sequestration of carbon by the biological CO_2 pump.

ing of biogenic particles (OC: SW→DW). This leads to decreased CO_2 concentration in surface waters. During early autumn, before freezing, the break-down of stratification favors invasion of atmospheric CO_2 into the SW to replace the lost C_T, hence a flux of CO_2 from the atmosphere into the ocean. Vertical mixing brings some deep CO_2 back towards the surface (LEGENDRE, 1996; not in the scheme of YAGER *et al.*, 1995). After the formation of sea ice (late autumn and winter), respiration in the water column exceeds primary production, which at this time of year is very low to nil because of the seasonal light cycle (see Section 2.1). This results in a net transfer of carbon from the organic to the inorganic pool (OC→C_T). However, because the ice acts as barrier to ocean-atmospheric exchanges, CO_2 produced during wintertime respiration is not lost back to the atmosphere. During spring, before ice melts, ice algal photosynthesis incorporates some of the accumulated CO_2 into organic carbon (C_T→OC). Following melting of the ice, a near-surface highly stratified layer forms which isolates the underlying water column from further air-sea gas exchange. At the same time, there is often massive downward export of ice algae (LEGENDRE, 1996; OC: SW→DW; not in the scheme of YAGER *et al.*, 1995).

In ice-free oceans, there is a net flux of CO_2 from the atmosphere to the water during spring-summer and a net flux from the ocean towards the atmosphere in autumn–winter. The two fluxes may balance each other, hence the net flux of CO_2 into the ocean may be small or null. In contrast, in seasonally ice-covered waters, there is a net flux of CO_2 from the atmosphere to the ocean surface during early autumn. However, the presence of ice cover from late autumn to early summer impedes sea-air exchange, so that CO_2 cannot return to the atmosphere. In spring, the CO_2 trapped in the under-ice water is fixed by ice algae, which are often massively exported to depth. Thus, at no time during the year can CO_2 escape to the atmosphere. This should result in net sequestration of carbon by the biological CO_2 pump.

The Arctic continental shelves are the site for most of primary production in the Arctic Ocean (Section 5.1 and LEGENDRE *et al.*, 1992). There is a seasonal flux of marine (*e.g.* ice algae, phytoplankton, and faecal pellets) and terrigenous (from riverine inputs) biogenic carbon to the bottom sediments of the shelves. Part of the accumulated organic matter is buried in sediments (local sequestration of biogenic carbon) and part is metabolized by benthic micro and macrofauna, thus releasing CO_2 in the overlying waters (ANDERSON *et al.*, 1990). Furthermore, since microbial degradation of sinking particulate organic matter is slower than in temperate oceans, the quantity and quality of organic particles available for ingestion in the water column or on the bottom is greater than in lower latitudes. During winter, the remineralized DIC in the bottom waters is transported across the shelf (Section 3.1; JONES and ANDERSON, 1986). ANDERSON *et al.* (1990) have shown that most of the carbon dissolved in shelf waters (*i.e.* introduced in the Arctic Ocean by river runoff and locally fixed by primary production) is transported into the halocline and the Atlantic layer, whereas little DIC reaches the Arctic Ocean Deep Water where it could be sequestered. Thus, most of the carbon not locally released to the atmosphere or sequestered on the Arctic Ocean shelves would be exported to the North Atlantic, where part is released to the atmosphere, part may be fixed by primary production in waters as it leaves the Arctic Ocean (*e.g.* in Fram Strait; ANDERSON *et al.*, 1990), and part could be incorporated in the North Atlantic Deep Water which is formed during

winter in the Greenland Sea (MORITZ *et al.*, 1990).

In addition to the biogenic carbon originating form shelf areas, the Fram Strait receives large amounts of organic matter transported by multi-year ice from the central basins of the Arctic Ocean. The Arctic ice pack accumulates organic matter over many years in the Beaufort Gyre and releases it upon melting in Fram Strait (MELNIKOV and PAVLOV, 1978; LARSSEN *et al.*, 1987; PFIRMAN *et al.*, 1989; HONJO, 1990). This could potentially increase the sequestration of biogenic carbon from the Arctic Ocean, by direct sedimentation of POC ($0.4–0.8\times10^6$ t of POC year^{-1}, MELNIKOV, 1989b, p. 62; 0.7×10^6 of sea-ice organisms year^{-1}, GULLIKSEN and LØNNE, 1989) and also by the same mechanisms as explained above (*e.g.* according to MELNIKOV, 1989b, p. 62, the sea ice transports $5.6–12.5\times10^6$ t year^{-1} of DOC through Fram Strait).

Thus, the two likely sinks for the sequestration of biogenic carbon produced on Arctic Ocean shelves are local sediments and the North Atlantic Deep Water. Although sedimentation of biogenic carbon appears to be greater inshore that offshore (Section 5.1), parallel gradients in benthic biomass, bioturbation and biological utilization and metabolism of the biogenic material in sediments should result in sequestration being lower inshore than offshore. In addition, the cross-shelf flow of near-bottom waters should favor shelf-basin transport of biogenic carbon from the offshore shelf waters towards the halocline, from which DIC can be exported towards the North Atlantic where it may be eventually sequestered. This pattern would be obviously much influenced by riverine inputs of inorganic and organic nutrients, local and cross-shelf circulation patterns, and the presence or not of polynyas on shelves.

7. Conclusion

The characteristics and factors regulating food webs are complex and are often influenced by both subtle and extreme differences in environmental conditions. Research in polar regions, including the Arctic Ocean, have been hampered by the very same environmental conditions which seem to be crucial in structuring pelagic ecosystems. Although ecosystem studies in the Arctic Ocean are not as comprehensive or as long-term as many in temperate latitudes, several patterns emerge. Based on our review of available studies, we propose that the extensive shelf system and riverine inputs influence the structure and dynamics of Arctic marine food webs in four ways. First the large freshwater runoff delivers particulate material and dissolved inorganic and organic nutrients, it lowers the salinity and favors the development of sea ice. Second, because of the extreme annual cycle of solar radiation, there is a brief pulse of primary production, which is often followed by a period of rapid sedimentation of POC. Third, because of low seawater temperature, there is slow oxidation of particulate organic matter in the water column and on the bottom. The latter provides a relatively steady supply of organic and inorganic nutrients for the year-round maintenance of a microbial trophic level in the water column. The low temperature may also favor efficient transfer of organic material from microbial components towards larger pelagic grazers and, ultimately, apex predators. Fourth, the seasonal ice cover constrains biological activity, provides a refuge and habitat for microorganisms and apex predators, and reduces ocean-atmosphere interactions thus favoring the sequestration of biogenic carbon.

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